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ARTICLE

Factors influencing the seasonal diet selection by woodland caribou (*Rangifer tarandus tarandus*) in boreal forests in Ontario

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Abstract: We used remote video cameras to assess seasonal diet composition of woodland caribou (*Rangifer tarandus tarandus* (L., 1758)) at three areas across the boreal forest of Ontario. Caribou consume lichens in winter, but we expected they would significantly reduce lichen consumption in favour of higher protein levels in green plants in summer. We sampled videos from 23 caribou, from 2 years, to derive seasonal diet composition. Diet differed among seasons and study areas, except in winter when lichens dominated. Diet breadth doubled from winter to summer, but overlap between seasons was still >60%. Green plants were less commonly eaten than we expected, only three genera were preferred, and few species constituted more than 2% of the diet. Preferred foods varied by land-cover types. Diet differed between managed and unmanaged landscapes but did not result from use of plant species found in successional habitats. Caribou selected a nonoptimal diet in the snow-free seasons, especially with respect to protein, suggesting factors other than nutrition influenced diet choice, and indicating the possibility of bottom-up limitation on production.

Key words: woodland caribou, boreal, diet selection, lichens, bottom-up limitation, *Rangifer tarandus tarandus*.

Résumé : Nous avons utilisé des caméras vidéo à distance pour évaluer la composition saisonnière du régime alimentaire du caribou forestier (*Rangifer tarandus tarandus* (L., 1758)) dans trois régions de la forêt boréale ontarienne. Les caribous consomment des lichens en hiver, mais il était attendu qu'ils réduiraient significativement leur consommation de lichens en été, pour se tourner vers les plantes vertes, qui offrent de plus fortes teneurs en protéines. Nous avons échantillonné des vidéos de 23 caribous sur 2 ans, afin de déterminer la composition saisonnière du régime alimentaire. Ce dernier variait selon la saison et la région étudiée, sauf en hiver, quand les lichens prédominaient. L'étendue du régime alimentaire était deux fois plus grande en été qu'en hiver, mais le chevauchement entre les saisons était néanmoins de >60 %. Les plantes vertes étaient moins largement consommées que prévu, seuls trois genres étaient privilégiés, et peu d'espèces constituaient plus de 2 % de l'alimentation. Les aliments privilégiés variaient selon le type de couverture du sol. Le régime alimentaire variait selon que le paysage faisait ou non l'objet d'une gestion, mais aucune différence ne découlait de l'utilisation d'espèces de plantes présentes dans les habitats de succession. Les caribous choisissaient un régime alimentaire non optimal durant les saisons sans neige, particulièrement en ce qui concerne les protéines, donnant à penser que des facteurs autres que la nutrition influencent les choix alimentaires et indiquant la possibilité d'une limitation ascendante de la production. [Traduit par la Rédaction]

Mots-clés : caribou forestier, boréal, choix du régime alimentaire, lichens, limitation ascendante, *Rangifer tarandus tarandus*.

Introduction

Woodland caribou (*Rangifer tarandus tarandus* (L., 1758)) is a threatened or endangered species depending on the jurisdiction in Canada. Although recovery planning has been instituted to try to conserve the species, reliable information on many aspects of basic life history and ecology is still lacking. One of the key uncertainties is diet selection and nutrition (Sleep 2007; Newmaster et al. 2013), although poor nutrition has been implicated as a cause of decline of caribou in some areas (Post and Klein 1999; Bastille-Rousseau et al. 2013). Most caribou ecologists consider the apparent competition hypothesis best explains observed caribou declines across Canada and there is substantial supporting evidence, albeit largely circumstantial in nature (Seip 1992; Wittmer et al. 2005; Festa-Bianchet et al. 2011; Pinard et al. 2012). Nevertheless, the current lack of understanding of caribou annual diet precludes a firm testing of alternate hypotheses related to food limitation and energetic concerns (Brown et al. 2007; Newmaster et al. 2013). Food intake is known to affect body mass, parturition, calf size, and calf survival (White 1983; Parker et al. 2005; Thompson and Barboza 2013). Female caribou do not always calve every year, are not known to produce twins, and calf survivorship is often low relative to other North American ungulates, including the other boreal ungulates. This suggests that poor nutrition is a plausible alternate hypothesis to explain declining populations either operating by itself, or synergistically with predation. Lack of knowledge about caribou diet also reduces our capacity to assess present range condition or understand the potential effects of climate change on caribou forage and energetics (Walsh et al. 1997; Lenart et al. 2002; Post et al. 2008). Understanding the annual diet is an essential step towards building an ecological energetics model for caribou to test hypotheses related to possible

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nutritional limitation on activity, parturition, habitat selection, and population size.

Caribou are known to rely heavily on lichens in winter and numerous studies have reported that percentage of lichens in the diet often exceeded 85%, based on direct or inferred observation (Schaefer and Pruitt 1991; Johnson et al. 2001), microhistology from scats (Thomas et al. 1994; Barten et al. 2001), DNA from scats (Newmaster et al. 2013), or by identification of rumen contents (Bergerud 1972). Although mountain caribou rely heavily on arboreal lichens (Rominger et al. 1996), boreal caribou seem to make relatively limited use of these species and feed most often on terrestrial lichens (Schaefer and Pruitt 1991; Newmaster et al. 2013). Most studies have also reported minor use of some plants in winter, including mosses, dead graminoids, ericaceous shrubs (genera *Ledum* (Labrador tea), *Chamaedaphne* (leatherleaf), *Kalmia* L. (laurel)), and limited browsing on deciduous shrubs (Bergerud 1972; Boertje 1990; Thomas et al. 1994; Johnson et al. 2001; Gustine et al. 2012). Nevertheless, more recent work by Newmaster et al. (2013) found more than 75 items were included in the winter diets of Ontario caribou based on DNA analysis and that there were differences among animals in their diet selection. This latter work indicated that even the winter diet of caribou, while dominated by lichens, is much more complex than was previously thought.

The only detailed examination of caribou diet during the snow-free period was from Newfoundland, where Bergerud (1972) reported seasonal diets from rumens (14–34 rumens per season). He found that sedges dominated in spring with just 9% terrestrial lichens; terrestrial lichens increased to 22% in summer, with fungi and shrub leaves accounting for 25% and 15%, respectively, and forbs accounted for another 8%, with a total green-plant composition of 43%; in fall, terrestrial lichens accounted for 38% with about 10% each of forbs, fungi, shrubs, and sedges; and in winter, arboreal lichens formed 54%, ground lichens just 2%, and evergreen shrubs 23% of the diet. Little other information is available about food plants selected during the snow-free period, including during the crucial lactating period for female caribou with newborn calves. Cringan (1957) observed plants being eaten by caribou on a large island in Lake Superior, Ontario, which included several common boreal forbs and shrubs. He also indicated that caribou used lichens, mosses, and fungi in the spring. A summer study of mountain caribou in the alpine zone in Alberta found that the diet consisted of 30%–55% terrestrial lichens, 16%–45% willow leaves, 10%–26% graminoids, 2%–3% *Ledum*, and 1%–4% *Equisetum* (horsetail) based on scat microhistology (Thomas et al. 1994). Finally, a study from Alaska reported a summer diet of 50% graminoids (both alive and dead), 25% deciduous shrubs, and 14% forbs, but few lichens, using microscopic analysis of fecal pellet contents (Barten et al. 2001). However, given the higher than expected complexity of winter diet suggested by Newmaster et al. (2013) and 35 species reported in the summer diet by Bergerud (1972), those few other studies likely under-represented diet breath.

Ungulate diet selection is governed by many factors including food content (e.g., fibre, protein, nutrients, secondary compounds) (Renecker and Schwartz 2007; Forsyth et al. 2005), forage availability (Danell and Ericson 1986), sex and age (Staines et al. 1982; Mysterud 2000), time of day (Newman et al. 1995), competition among ungulate species (Dailey et al. 1984), and plant phenology (Bee et al. 2010; Zweifel-Schielly et al. 2012). Other behavioural factors related to avoiding hunters, predators, and insects may also play a role in habitat selection, which may affect diet selection (Belovsky 1991; Skogland 1991; Newman et al. 1995). Simple comparisons of nutritional characteristics suggest that, although caribou are known to eat predominantly lichens in winter, they should switch almost entirely to green plants in summer, as is known to be the case for other boreal ungulates (Renecker and Schwartz 2007; Berteaux et al. 1998) because of much higher protein and lower fibre levels in new green vegetation than in lichens. Such a switch would be consistent with optimal foraging models that predict herbivores should detect and use the best available nutrition (Belovsky 1984; Owen-Smith and Novellie 1982). One might also expect that parturient females with their high energy demands (Parker et al. 2009) might be particularly selective for habitats that both avoid predators but also enhance forage quality, leading to the prediction that diets of females with calves should differ from females that did not calf or that lost calves early (Barten et al. 2001; Lantin et al. 2003).

Forest management is understood to reduce the availability of habitat to woodland caribou because of the reduction in the area of preferred old forest on the landscape (Courtois et al. 2007; Hins et al. 2009) and because of the use of these disturbed habitats by predators (Seip 1992; Wittmer et al. 2005). Caribou avoid managed habitats (e.g., Hins et al. 2009), although Ferguson and Elkie (2004) reported nonavoidance of managed areas for travelling. Successional boreal landscapes result in different foraging opportunities for ungulates. In particular, there is an increase in shrub biomass and forb species and biomass for at least 20 years, many of which differ from species that are available in old forest habitats (Carleton 2000; Chen and Popadiouck 2002). We were interested in whether or not caribou diets differed between partly managed and unmanaged landscapes, and if so, how and why they differed in response to the creation of successional habitats following forest management.

It is impossible to observe foraging boreal caribou in the wild, because the animals occur at very low densities, are extremely wary of humans, and avoid open areas and areas with roads. Therefore, we undertook to determine annual diet selection using remote video camera recorders attached to radio collars (Thompson et al. 2012; Newmaster et al. 2013). Using this remote sensing system, we examined caribou diets from three different areas of Ontario to answer three main questions. First, is caribou diet uniform across Ontario's boreal forest? Second, how does woodland caribou diet change seasonally? Finally, does caribou diet differ between managed and unmanaged forest landscapes?

Materials and methods

Study areas and radio-collaring protocol

We studied diet selection at three study areas in northern Ontario, separated from east to west by 700 km. Each study area covered approximately 23 000 km², in areas north of Cochrane, Nakina, and Pickle Lake, Ontario. All three study areas were in the boreal zone, dominated by black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.), jack pine (*Pinus banksiana* Lamb.), trembling aspen (*Populus tremuloides* Michx.), white birch (*Betula papyrifera* Marsh.), and balsam fir (*Abies balsamea* (L.) Mill.) (Rowe 1972). Contrasting disturbance regimes at each area has resulted in different proportions of these dominant tree species in the local forests. Of the total land area, the Pickle Lake study area was 37% coniferous, 11% mixedwood, and <1% deciduous forest, about 12% had been burned by wildfires in the last 50 years, but there had been no logging. The study area near Nakina had 29% conifer, 24% mixedwood, and 6% deciduous forest, with approximately 5% of the area burned over the preceding 50 years, while the total harvested area was 28%. The Cochrane study area was 45% conifer, 9% mixedwood, and 1% deciduous forest, with 4% of the area disturbed by fire in the last 50 years, and there was 13% harvested area. Notably, the northern half of the Cochrane study area was largely undisturbed, making the area a mixture of managed and unmanaged forests. The Cochrane area was situated on lacustrine soils, with limited relief and highly interrupted drainage and had about 13% in bogs or fens with few lakes. Both the other areas had rolling topography and till soils, with <8% in bogs and fens but many lakes.

Adult female woodland caribou were captured by a commercial large animal capture company using a helicopter and net gun in March 2011 and 2012. Capture and collaring procedures followed

Canadian Council on Animal Care (2003) "Guidelines on the care and use of wildlife" and were approved by the Ontario Ministry of Natural Resources Animal Care Committee (protocol 11-183). We deployed 26 GPS camera collars on caribou over the 2 years. The cameras were housed in a hard plastic case suspended from an upper modified GPS satellite collar housing (model GPS7000MA; Lotek Wireless Inc., Newmarket, Ontario, Canada), which included an Argos transmitter for remote data uplink, and a back-up VHF beacon with mortality sensors for collar recovery. GPS locations were acquired hourly, activity was recorded at 5 min intervals, and the data were uploaded to Argos satellites every 2 days.

Feeding and other activities were recorded by the remote video camera units (Thompson et al. 2012). We programmed the video cameras to record 10 s video segments every 5 min on a duty cycle from 0800 to 1000 and again from 1500 to 1700 each day. The total video data storage capacity was 32 or 64 GB and other limitations were provided by battery size and optimal collar mass. Our choice of recording time and battery size enabled recording for a 36-week period from late winter to fall. Each video recording was labelled electronically with a file number, date, and time. Video data were too large to use the satellite uplink for retrieval, so we had to recover the collars to obtain the data cards. In 2011–2012, automatic drop-off mechanisms were deployed on camera collars. When the mortality signal was obtained (indicating 16 h of inactivity), a crew was dispatched to recover the collar either by aircraft or by vehicle if the collar was within 5 km of a road. In 2012–2013, all the drop-off mechanisms failed and the caribou had to be recaptured to obtain the data. We downloaded the video data from the camera cards and GPS locations and activity data from the radio collars to a spreadsheet program. Other technical details about the video camera units were provided in Thompson et al. (2012).

Sampling of video data

Data were downloaded from the 23 caribou camera collars recovered and all videos were viewed to create a subset of those with feeding events. There were 18 325 and 16 738 videos that contained feeding events in 2011 and 2012, respectively. Conducting identifications for all feeding videos was not possible because of available time for observers, so we randomly sampled up to 200 videos for each caribou for each season, resulting in 13 443 samples of feeding behavior.

To make decisions about transition between seasons, we used images from remote cameras that took pictures of metre sticks in forest stands at each study area at 1100 each day from mid-September to mid-July. We defined winter as the time period when there was snow cover, with the thresholds arbitrarily set as >10 cm snow cover during the fall to winter transition and >50% ground snow cover for the winter to spring transition. Spring was defined as the period after the snow melted but before the majority of plants had leaves. It was clear from snowfall cover data and the feeding videos that the availability of green plants changed considerably from early to late spring. Therefore, we subdivided spring into early and late periods based on the appearance of the first green plants, which were graminoids occurring about 3 weeks prior to the majority of green plants, especially shrub leaves. We defined summer as the period of time from initial leaf-out of deciduous shrubs to the time when the chloroplasts began to die. Fall was the time between summer and winter characterized by little green vegetation other than mosses and with minimal snow cover.

After a short training period, six experts at boreal forest plant identification recorded the vegetation consumed from video clips to the most precise identification possible (almost always to genus and most to species), the number of bites taken, along with the time and date. We defined bites as an individual jaw movement of a caribou as it consumed food items. Foods were recorded as genus, species, and functional groups (terrestrial lichens, arboreal lichens, mosses, graminoids, forbs, ericaceous shrubs, fern allies, and deciduous shrubs).

Observer variability was assessed by presenting each with the same set of 34 videos to analyze. Bite counts were compared using a generalized linear model with bites as the response variable, observers as the explanatory variable, and a Poisson distribution with log-link. Comparisons of the identification of functional groups were made by establishing a correct answer for each video and grading the observers according to their answers. There were significant differences in bite counts among observers, therefore we used the model to apply a correction factor to the results for two observers, while four observers required no corrections. Our observers correctly identified the food items consumed 85.3% of the time for species, 86.4% for genus, and 94.4% for the functional groups. In the latter case, the few errors were mostly associated with differences in opinion about whether dead graminoids were classified as graminoids or as litter.

Bite size results in different biomass consumed depending on the food type eaten by caribou (Trudell and White 1981). Biomass consumed is a more appropriate measure of diet than bites taken and so we applied correction factors to number of bites taken, based on measured dry biomass consumed per bite from Trudell and White (1981): for mosses and lichens of 32 mg/bite and for vascular plants and fungi of 21 mg/bite.

Plant species availability

We sampled plant species availability at Nakina but not for Cochrane or Pickle Lake because of budgetary constraints. The majority of the study areas were classified using the Ontario Far North Land Cover version 1.3.1 (FNLC), based on Landsat imagery collected between 2006 and 2009. Southern portions of the study areas were classified using the Provincial Land Cover database (PLC 2000), 2nd edition (Ontario Ministry of Natural Resources 2000), which is a Landsat-derived product. Land-cover types that represented lowlands were aggregated into two classes (open and treed lowlands) and classes representing disturbances were pooled into two classes (those with and without large trees). We used eight vegetated land-cover classes for sampling: open lowlands, treed lowlands, sparse forest, deciduous forest, conifer forest, mixed forest, and two disturbance types. The "disturbance" type in FNLC included areas that were harvested or burned from 1952 to present. We also distinguished between harvested and burned sites, however, using the forest resource inventory mapping that was done from aerial photographs.

We derived the polygon used by all caribou with radio collars at the Nakina study area using the GPS collar data and then used the area of each land-cover class within that large polygon to weight the availability of abundance of each plant and lichen species. Stands in each of the eight land-cover types were sampled for available food taxa by random selection from within the area used by the radio-collared caribou, but restricted to those stands occurring within 2 km of available access. Diet species were sampled in each of the land-cover types on 2–8 stands, although we sampled the "disturbed" cover types on 25 stands to include a range of forest ages, which were then pooled into >30 and <30 years of age (because these could be distinguished on the satellite imagery). Terrestrial and arboreal lichen biomass and percent cover data were collected using the methods of McMullin et al. (2011). For terrestrial lichens, we observed from the videos that caribou only grazed the top 1 cm or at most 2 cm, and left the rest of the structures in all cases, based on a sample of several thousands of bites. Our terrestrial lichen biomass estimates were accordingly calculated based on the top 2 cm. Plant availability was sampled by assessing percent ground cover of each plant species up to a height of 2 m on four to six 1 m^2 quadrats per stand for each major land-cover type. We could not always identify graminoids to species from the feeding videos and so their availability was also pooled as a category (functional group) for this taxon only while

Table 1. Number of woodland caribou (*Rangifer tarandus tarandus*) and 10 s video segments that were used to define diet selection by season for each of the three study areas.

		Winter		Early spring		Late spring		Summer		Fall	
Study area	Year	Caribou	Video	Caribou	Video	Caribou	Video	Caribou	Video	Caribou	Video
Nakina	2011	5	809	4	469	4	614	3	910	0	
Cochrane	2011	5	1051	3	269	3	453	3	604	0	
Pickle lake	2011	5	841	2	184	2	326	2	141	0	
Nakina	2012	3	417	3	425	1	77	1	66	0	
Cochrane	2012	3	299	6	807	6	454	6	1214	4	812
Pickle Lake	2012	2	290	5	839	3	185	3	472	2	416
Total		23	3707	23	2993	19	2109	18	3407	6	1228

all the others were analysed as genera. We also pooled available foods into the functional groups (above) for a second analysis of electivity.

Data analysis

We sampled diet choice from a large number of videos (e.g., >350) from five caribou per season (except fall) per year to generate rarefaction curves using the vegan package (version 2.0-10; available from http://cran.r-project.org/web/packages/vegan/, accessed 16 December 2013) to estimate the sample size that would include most of the food species consumed by a caribou in each season. Rarefaction curves attained an asymptote for species eaten with about 200 video samples in early and late spring, summer, and fall, and with about 150 samples in winter. We attempted to sample up to 200 videos per caribou per season, although videos from all seasons were not equally available for all caribou owing to mortalities, camera programming errors, and variable battery life. From both years, 89 caribou seasons were completed.

We calculated diet diversity for the genus level for five seasons (including two spring periods) and three study areas using Levins' (1968) index, and examined food niche overlap among study areas and seasons with Schoener's (1970) index. We used Vanderploeg and Scavia's (1979) electivity index to assess selection of individual genera and functional groups in the diet in late spring and summer for the entire landscape, and also within each land-cover type that comprised >5% of the landscape.

We conducted separate statistical analyses for food items identified at the genus level, and for the functional groups, to determine differences among seasons and study areas. We used the program R to conduct linear discriminant analysis with package MASS (version 7.3-29; available from http://cran.r-project.org/web/packages/MASS/index.html, accessed 15 December 2013) and visualized using the candisc package (version 0.6-5; available from http://cran.r-project.org/web/packages/candisc/, accessed 15 December 2013). We interpreted the discriminant analyses by examining the successful reclassification of bootstrapped cases, as well as by significance level of the models. Samples were caribou seasons and variables were the total grams of each food item divided by the total grams consumed for that caribou season (i.e., proportion of an item in the diet). The diet data were arcsine square-root transformed to achieve multivariate normality. Following sample size guidelines suggested by Williams and Titus (1988), we limited the number of variables used in our analyses to the eight most abundant food items eaten by caribou for comparisons among study areas and to the seven most abundant foods for the comparisons among seasons.

Results

We recorded caribou diet based on 249 012 bites taken over 2 years, by 23 caribou, converted to an index of milligrams of dry biomass per bite, with the sample spread among the three study areas and five seasons (Table 1). Our sample size was from four to nine caribou depending on season and area and was based on 1228–3707 video segments. The sample from fall was limited to two of our three study areas. We compared diet between years and between morning and evening and found no differences in diet for either plant functional group or genus (both values of $P > 0.74$), so videos for each caribou within a season were combined and seasons were combined for the 2 years. We recorded 74 genera with 89 species eaten by caribou in Ontario. At the species level, we observed at least 72 species (including several only as genera) and 67 genera/species eaten in summer and winter, respectively, combined for all caribou. We were able to identify species for most lichens and some graminoids but not from all videos, so diet was analysed at the genus level. Many items occurred rarely in the diet and, considering only genera that constituted at least 1.5% of the total diet, the number of items changed little by season ranging from 9 in winter to 11 in summer, including just 15 genera plus the graminoids and fungi (Table 2, Figs. 1 and 2). Several items were recorded as eaten but were not included in our analyses, including litter, bark, animal scats, unidentified aquatic macrophytes, water, and snow.

Seasonal diet

Woodland caribou diet was dominated by terrestrial lichens (mostly *Cladina* spp. (reindeer lichen)), ranging from a low of 46% of food consumed in summer to >70% in winter, while arboreal lichens comprised just under 7% in winter (Table 2, Fig. 2). Among the other plants, graminoids were important primarily in spring, although they were eaten in all seasons including dead stalks in winter. We observed little browsing on shrubs in winter and the leaves of several shrub species were rarely eaten, mostly in late spring. *Maianthemum trifolium* (threeleaf false lily of the valley) was the most common forb eaten, constituting 13.5% of biomass taken in summer (Table 3). The overall index of diet diversity indicated that diet breadth doubled from winter to summer, but with a high overlap index of >66% with each subsequent season. The least annual seasonal overlap was 62% between winter and summer among all areas combined, while there was a high similarity between fall and winter diets (Table 4). Mosses were little consumed, with *Sphagnum* spp. as the most common genus, mostly eaten in early spring prior to other green plants becoming available.

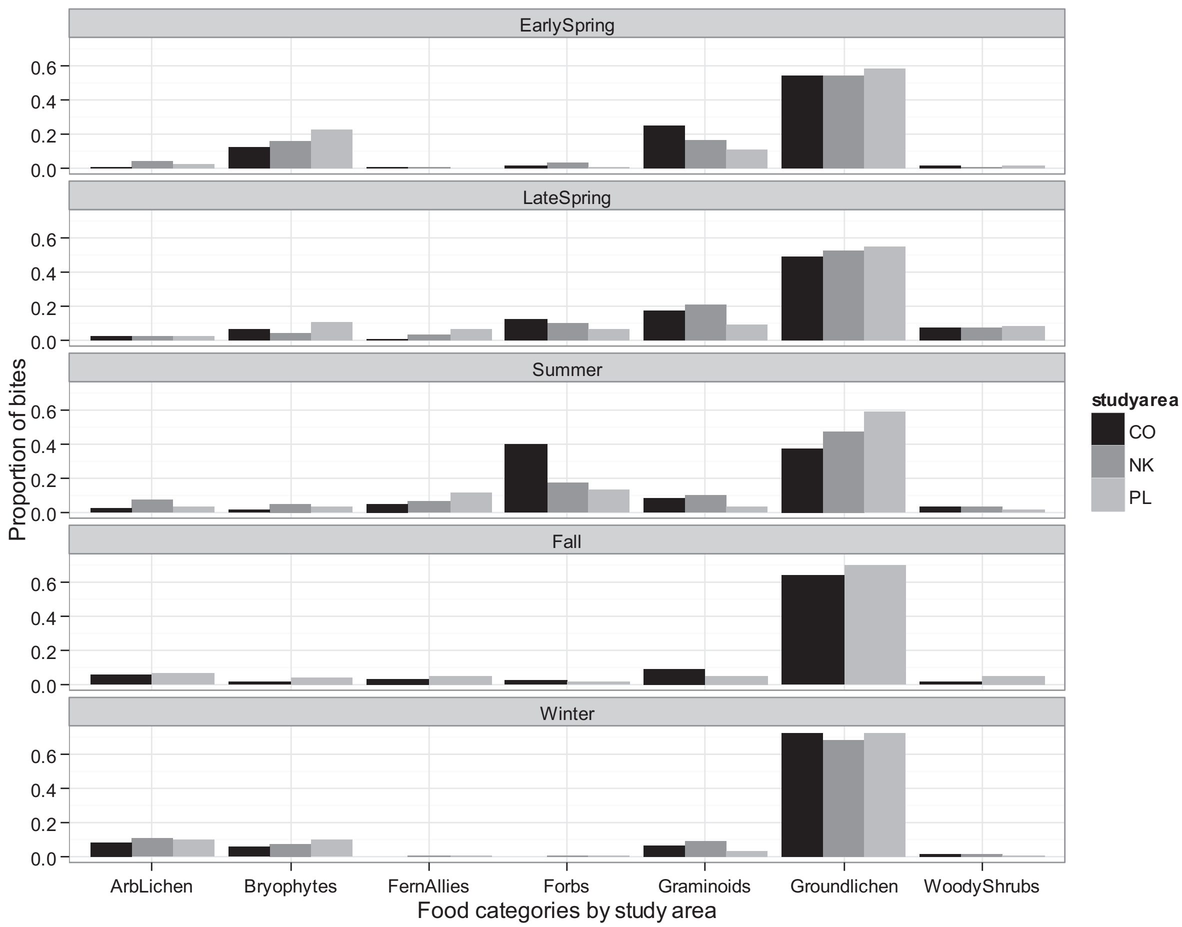
Despite the apparent high overlap in diet selection among some seasons (with fall excluded), the discriminant analysis found key functional groups that differentiated caribou seasonal diets, including graminoids, forbs, fern allies, and lichens (Fig. 3). The significant model ($F_{[3,21]} = 19.0$, $P < 0.001$) for seasons correctly classified 78%–96% of the cases and the first two eigenvectors explained 97% of the variance. Similarly, a significant discriminant analysis with genera ($F_{[3,21]} = 17.8$, $P < 0.001$) correctly classified the season for 78%–89% of the cases, with two eigenvectors explaining 98% of the variance (Fig. 3). A second model that included fall for Pickle Lake and Cochrane was also significant ($F_{[4,28]} = 11.3$, $P < 0.001$) and correctly classified 81%–100% of the cases correctly. For functional groups, with fall data for Pickle Lake and Cochrane, the discriminant function model was significant

Table 2. Main diet items by genus or functional group eaten by woodland caribou (*Rangifer tarandus tarandus*) by season in Ontario expressed as proportion (SE) of total grams consumed recorded from videos for each season.

Genus, functional group, and common name	Winter (2216 g consumed)	Early spring (1574 g consumed)	Late spring (1006 g consumed)	Summer (1536 g consumed)	Fall (684 g consumed)
Cladina (Nyl) Nyl., reindeer lichen	0.76 (0.05)	0.61 (0.02)	0.59 (0.02)	0.54 (0.03)	0.73 (0.02)
Graminoids	0.03 (0.01)	0.12 (0.02)	0.11 (0.02)	0.05 (0.01)	0.05 (0.01)
Maianthemum F.H. Wigg., mayflower	NA	<0.01	0.05 (0.01)	0.15 (0.03)	<0.01
Sphagnum L., sphagnum moss	0.02 (0.01)	0.11 (0.02)	0.02 (0.01)	<0.01	0.01 (0.01)
Equisetum L., horsetail	<0.01	<0.01	0.01 (0.01)	0.05 (0.01)	0.02 (<0.01)
Fungi	NA	NA	NA	0.05 (0.02)	0.03 (0.01)
Pleurozium Mitt., big red stem moss	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)	<0.01
Evernia Ach., ring lichen	0.01 (<0.01)	<0.01	<0.01	<0.01	0.02 (0.01)
Chamaedaphne Moench, leatherleaf	0.01 (<0.01)	<0.01	0.01 (<0.01)	<0.01	0.01 (0.01)
Menyanthes L., buckbean	NA	<0.01	<0.01	0.02 (0.01)	<0.01
Usnea Dill. Ex Adans., beard lichen	0.01 (<0.01)	<0.01	<0.01	<0.01	<0.01
Bryoria Brodo & D. Hawksw., horsehair lichen	0.01 (<0.01)	<0.01	<0.01	<0.01	<0.01
Ledum L., Labrador tea	<0.01	<0.01	<0.01	<0.01	0.01 (<0.01)
Salix L., willow	<0.01	<0.01	0.01 (0.01)	<0.01	<0.01
Alnus Mill., alder	<0.01	<0.01	0.01 (<0.01)	<0.01	<0.01
Clintonia Raf., bluebead	<0.01	<0.01	<0.01	0.01 (<0.01)	<0.01
Betula L., birch	<0.01	<0.01	0.01 (<0.01)	<0.01	<0.01

Note: Sample size of number of bites ranged from 24 100 in fall to 73 133 in summer. NA indicates not available in the season.

Fig. 1. Diet composition of woodland caribou (*Rangifer tarandus tarandus*) by bites taken for five seasons at three study areas in Ontario, 2011–2013. NK, Nakina; CO, Cochrane; PL, Pickle Lake.



($F_{[4,28]}$ = 13.1, P < 0.001) and correctly classified 81%–100% of the cases.

Seasonal diet among study areas

Diet choice varied among the study areas (Fig. 4) for all seasons combined and by season. The lowest summer diet breadth was at the unmanaged Pickle Lake area, where the diet breadth was more similar between seasons than at either of the other study areas (Tables 4 and 5, Figs. 1 and 2). Diet breadth was most similar among study areas in winter, when overlap was almost 90%, but similarity declined through spring and summer to about 70% (Table 5). Caribou at Cochrane had the highest diet diversity during each of the snow-free seasons, compared with animals at the other areas. Diet overlap was higher between Pickle Lake

Fig. 2. Diet composition of woodland caribou (*Rangifer tarandus tarandus*) by dry biomass consumed for five seasons at three study areas in Ontario, 2011–2013. NK, Nakina; CO, Cochrane; PL, Pickle Lake.

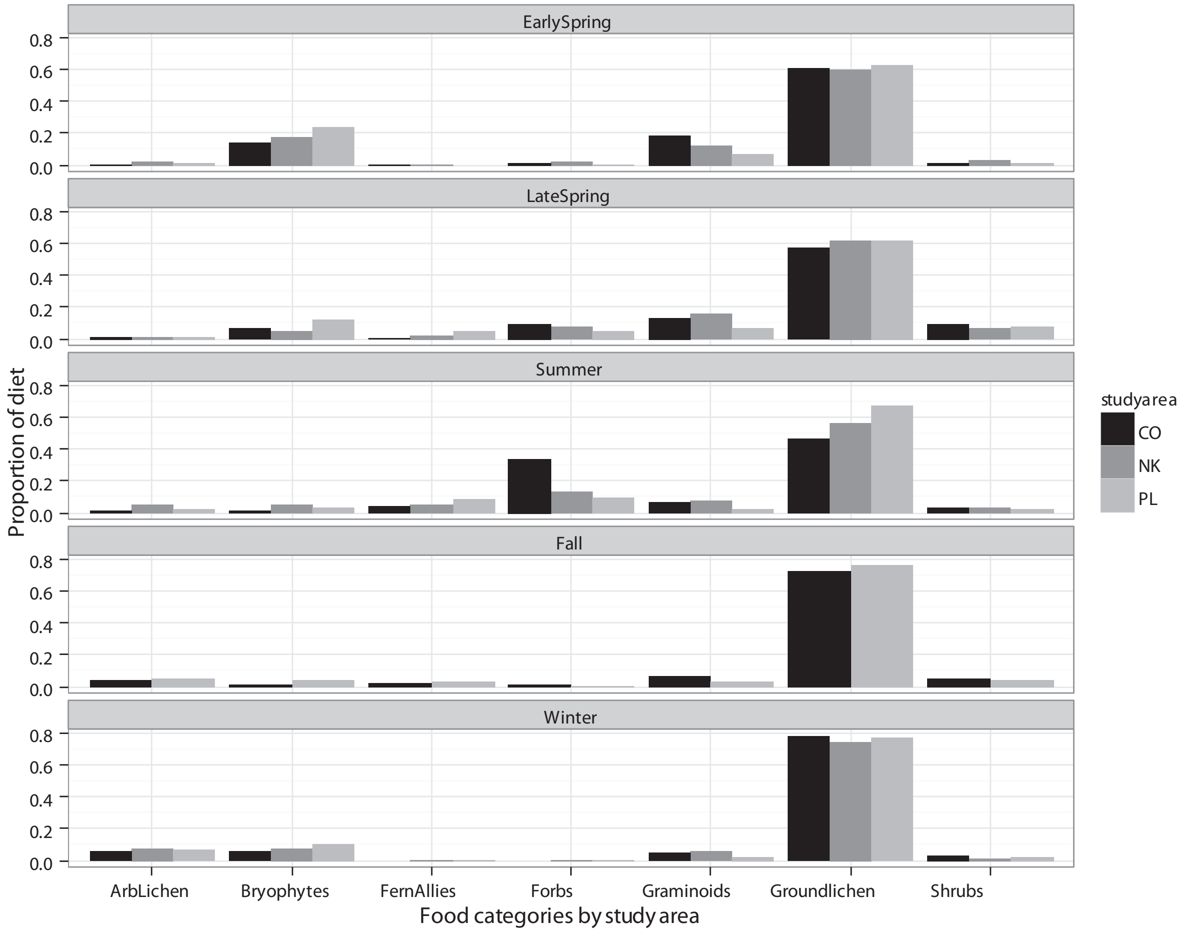


Table 3. Comparison among the three Ontario study areas of percent consumed of summer food species or functional group by woodland caribou (*Rangifer tarandus tarandus*) that comprised at least 1.5% of the diet for at least one of the three areas.

Diet item	Pickle Lake	Nakina	Cochrane
Lichens			
Cladina rangiferina (L.) Nyl., greygreen reindeer lichen	49.97	63.33	40.34
Cladina stellaris (Opiz) Brodo, star reindeer lichen	14.52	1.11	3.12
Cladina spp., reindeer lichen	3.52	0.04	1.71
Usnea spp., beard lichen	0.19	2.59	0.01
Graminoids	1.90	7.84	6.46
Forbs and fern allies			
Maianthemum trifolium (L.) Sloboda, threeleaf false lily of the valley	8.62	6.17	25.68
Maianthemum canadense Desf., Canada mayflower	0.00	2.05	0.08
Equisetum spp., horsetail	5.55	1.30	2.43
Menyanthes trifoliata L., buckbean	0.01	0.24	5.95
Clintonia borealis (Aiton) Raf., bluebead	0.25	1.52	1.16
Mosses			
Pleurozium schreberi (Brid.) Mitt., Schreber's big red stem moss	1.71	1.79	0.25
Other plants	13.76	12.03	12.81

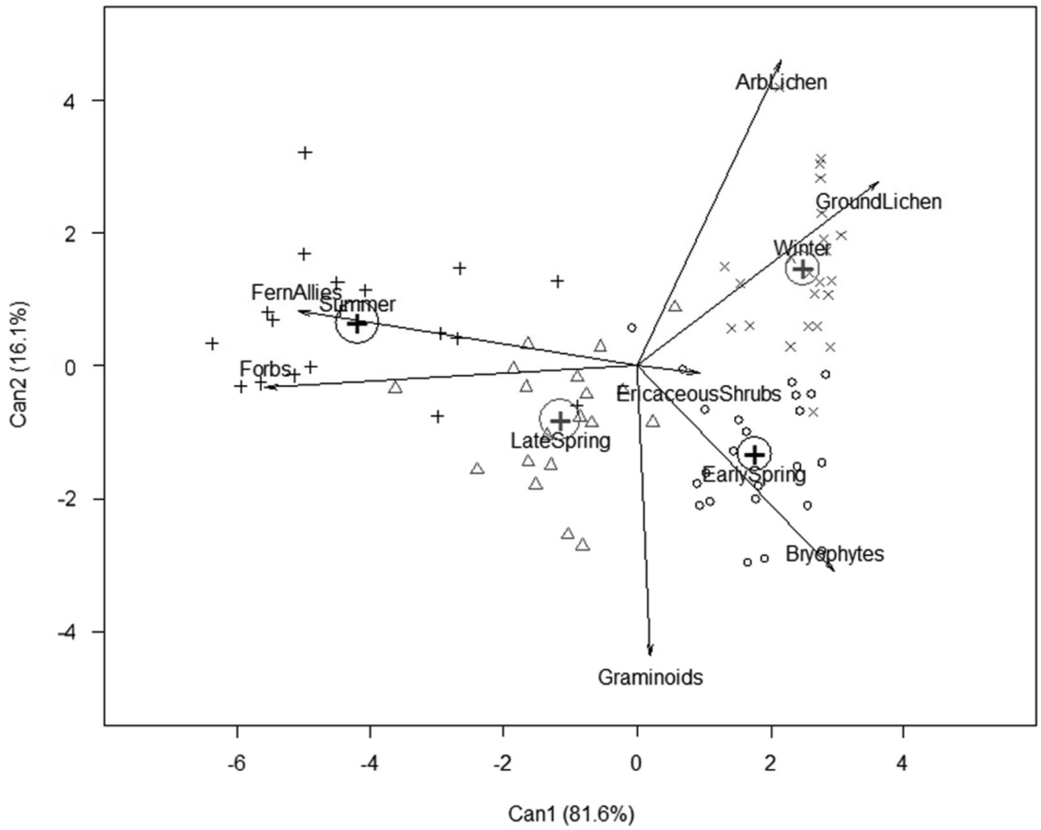
and Nakina than between Pickle Lake and Cochrane, while diet was most dissimilar between Cochrane and Nakina in summer (Table 3).

We were unable to discriminate winter diet selection among study areas by functional groups or genera (all P values > 0.25). For early spring, the genus-level model was not significant ($P = 0.16$), although the model for functional groups was significant ($F_{[2,10]} = 3.0$, $P = 0.009$). The latter model correctly classified diets 57% of the time for Nakina and Pickle Lake, and for 67% of caribou in Cochrane. Significant models for functional groups ($F_{[2,10]} = 4.3$, $P < 0.001$) and genera ($F_{[2,10]} = 3.9$, $P < 0.001$) were found for late-spring and summer seasons combined. Nevertheless, correct classification for Nakina was low at 44% using functional groups and 22% using genus. Correct classification exceeded 67% in both models for late spring + summer caribou diet at Pickle Lake and Cochrane (Table 3, Fig. 4).

Table 4. Woodland caribou diet breadth (Levin's index) and seasonal proportional overlap (Schoener's index) for all woodland caribou (*Rangifer tarandus tarandus*) from the three study areas over 2 years and seasonal diet breadths.

	Winter	Early spring	Late spring	Summer	Fall
Overall diet breadth	1.973	2.861	3.352	4.127	2.314
Overall overlap with following season	0.767	0.797	0.715	0.667	0.868
Pickle lake	2.00	2.63	3.12	2.74	2.02
Nakina	2.12	3.01	3.06	4.05	NA
Cochrane	1.81	2.86	3.56	4.24	2.44

Fig. 3. Discriminant analysis ordination of woodland caribou (*Rangifer tarandus tarandus*) diet composition among seasons for plant functional groups. Vectors illustrate variables that strongly loaded for each season and **+** sign is the season centroid.



The best comparison of diet in unmanaged and managed forest areas was between the Pickle Lake (no harvesting) and the Nakina (28% harvested) study areas, because those areas are relatively close and had less lowland area than the Cochrane area. Diet breadth during summer was about 50% lower at Pickle Lake than at Nakina, while winter and spring diet breaths were similar (Table 3), and summer overlap was about 78% (Table 4). Main diet differences included more graminoids in the diet at Nakina and more *Cladina stellaris* (star reindeer lichen), *Equisetum*, and *Maianthemum trifolium* in the diet at Pickle Lake, none of which reflected the logging at Nakina. Among species that were abundant at Nakina as a result of forest management, one forb (*Aster ciliolatus* (Lindl.) Á. Löve & D. Löve (Lindley's aster)) and four shrubs (*Ribes triste* Pall. (red currant), *Sambucus nigra* L. ssp. *canadensis* (L.) R. Bolli (American black elderberry), *Rosa acicularis* Lindl. (prickly rose), and *Diervilla lonicera* Mill. (northern bush honeysuckle)) were eaten and together comprised 0.7% of the diet, and were not eaten at Pickle Lake. No species that was only abundant in young managed forest stands (e.g., leaves from *Acer spicatum* Lam. (mountain maple) or *Corylus cornuta* Marshall (beaked hazelnut)) was common in the diet of caribou at Nakina (Table 3).

Diet electivity

Electivity indices for diet items from late spring and summer at Nakina showed that only a few species were selected and that only some lichens were strongly selected at the study-area scale (Table 6). Electivity changed from late spring to summer as a result of different and broader diet choices, partly as a result of phenology (e.g., *Menyanthes* (buckbean) was not available until summer). No forbs were selected. Among the shrubs, *Betula* (birch) and *Amelanchier* Medik. (serviceberry) were selected in spring and *Diervilla* (bush honeysuckle) was selected in summer, while no ericaceous shrub was selected. None of the mosses was selected and these plants may have been consumed incidentally with lichens. *Equisetum* was selected more in summer than in late spring. Among the functional groups, only arboreal lichens were selected (late spring 0.77; summer 0.76). Electivity was not correlated to percent cover of food items (all P values > 0.3).

Electivity indices at the smaller scale of land-cover types revealed that food preferences differed among the types, which reflected differential plant availability (Table 7). *Cladina* was selected in both seasons (late spring and summer) in all habitats except in "disturbed treed" habitats. Other lichens were selected

Fig. 4. Discriminant analysis ordination of woodland caribou (*Rangifer tarandus tarandus*) diet composition among study areas for plant functional groups, with all seasons combined (NK, Nakina; PL, Pickle Lake; CO, Cochrane). Vectors illustrate variables that strongly loaded for each area and **+** sign is the centroid for the study area.

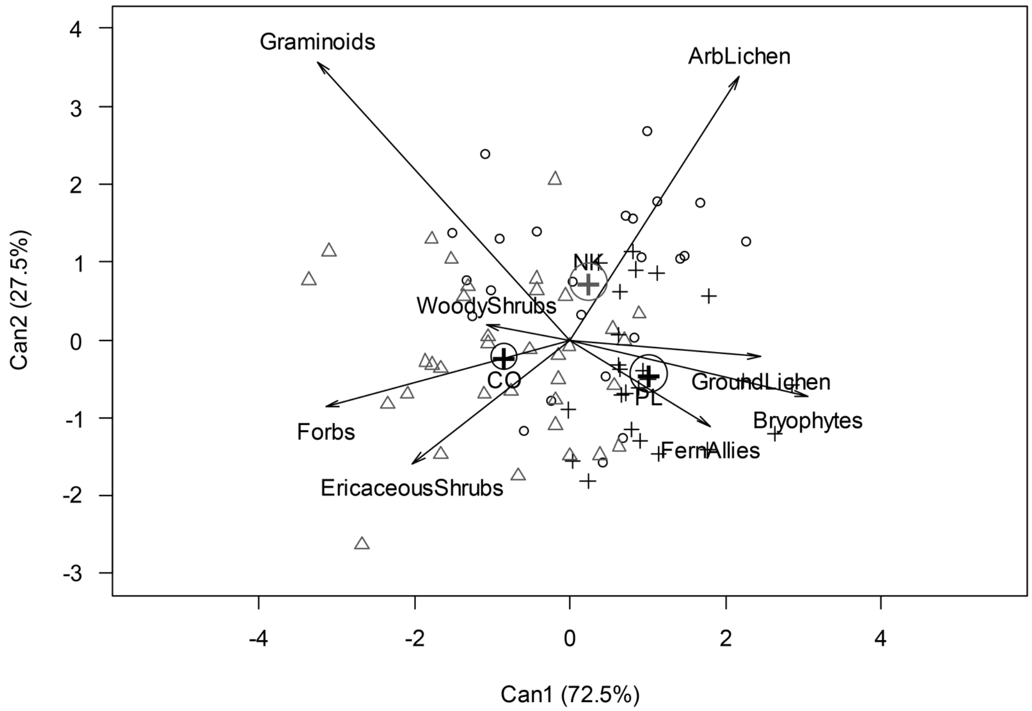


Table 5. Woodland caribou (*Rangifer tarandus tarandus*) diet similarity among the study areas by seasons.

Study area comparison	Winter	Early spring	Late spring	Summer	Fall
Pickle Lake vs. Cochrane	0.904	0.814	0.760	0.653	0.827
Pickle Lake vs. Nakina	0.895	0.870	0.779	0.775	NA
Cochrane vs. Nakina	0.868	0.877	0.809	0.694	NA

Note: Values reported are Schoener's (1970) index of proportional overlap (range 0–1).

mostly in "bog and treed bog" and in "conifer", although less selected in spring than in summer. Grasses and sedges were selected in spring and (or) summer in "bogs and treed bogs", except specifically *Carex* (sedge), which was not selected. Among the few forbs and fern allies that were selected, *Maianthemum* (mayflower) was selected in "fens" and in late spring in "disturbed treed" habitats, *Menyanthes* and *Clintonia* (bluebead) were mostly available in summer and only selected on "bog and treed bog" areas despite widespread availability of *Clintonia* in all habitats, *Aralia* (spikenard) was selected in "disturbed treed" habitats, and *Equisetum* was selected in summer in "mixedwoods". Caribou only selectively foraged on two shrubs: *Salix* in late spring in "bog and treed bogs" and *Diervilla* in summer in "conifer" habitat. None of the mosses or ericaceous shrubs was selected in any habitat.

Discussion

Our study presents the most comprehensive diet information available for woodland caribou recorded from mainland boreal forests in Canada and one of only two studies on annual diet selection. Overall, the use of up to 80 diet items suggests an eclectic diet but, in fact, just six or seven species comprised the majority of the foods eaten in any season, including in summer when more than 130 species of forbs alone were commonly available on our study areas. While the sample of individual animals was somewhat small in some seasons and areas, it likely had limited effect

Table 6. Electivity values (Vanderploeg and Scavia's index) of the main food items (>0.5% in diet) eaten in late spring and summer by woodland caribou (*Rangifer tarandus tarandus*) for the Nakina study area.

	Electivity	
Functional group, genus, and common name	Late spring	Summer
Lichens		
Cladina, reindeer lichen	**0.86**	**0.80**
Cladonia P. Brown, cup lichen	**0.72**	**0.67**
Usnea, beard lichen	−0.13	**0.58**
Bryoria, horsehair lichen	−0.21	**0.25**
Evernia, ring lichen	−0.01	**0.45**
Graminoids*	−0.15	−0.62
Forbs and fern allies		
Maianthemum, mayflower	−0.77	−0.74
Aralia L., spikenard	−0.89	−0.75
Menyanthes, buckbean	NA	−0.39
Clintonia, bluebead	−0.70	−0.64
Cornus L., dogwood	−0.95	−0.98
Equisetum, horsetail	−0.02	**0.23**
Shrubs		
Salix, willow	−0.68	−1.00
Alnus, alder	−0.95	−0.99
Betula, birch	**0.76**	−1.00
Diervilla Mill., bush honeysuckle	−1.00	**0.82**
Vaccinium L., blueberry	−0.99	−1.00
Ericaceous shrubs		
Chamaedaphne, leatherleaf	−0.92	−0.99
Ledum, Labrador tea	−0.98	−1.00
Mosses		
Sphagnum, sphagnum moss	−0.99	−0.98
Pleurozium, big red stem moss	−0.99	−0.98
Ptilium De Not., ptilium moss	−0.86	−0.96
Hylocomium Schimp., hylocomium feather moss	−0.99	−1.00

Note: All other genera had an electivity index of <0. Positive electivities are set in boldface type. NA indicates not available in spring.

*Includes grasses and sedges (only some *Carex* spp. were identified).

Table 7. Electivity values (Vanderploeg and Scavia's index) for genera eaten in late spring and summer by woodland caribou (*Rangifer tarandus tarandus*) within the major land-cover types on the Nakina study area.

Functional group, genus, and common name	Fen: Late spring	Fen: Summer	Bog and treed bog: Late spring	Bog and treed bog: Summer	Conifer: Late spring	Conifer: Summer	Mixedwood* (summer)	Disturbed open† (late spring)	Disturbed treed† (late spring)
Lichens									
Cladina, reindeer lichecn	**0.93**	**0.82**	**0.91**	**0.85**	**0.96**	**0.95**	**0.94**	**0.96**	−1.0
Cladonia, cup lichen	−1.0	−1.0	**0.76**	**0.39**	**0.67**	**0.60**	−1.0	−1.0	−1.0
Usnea, beard lichen	−1.0	**0.83**	**0.21**	**0.87**	−0.36	**0.36**	−1.0	−1.0	−1.0
Bryoria, horsehair lichen	−1.0	−1.0	−1.0	**0.40**	−0.32	**0.16**	−1.0	−1.0	−1.0
Evernia, ring lichen	−1.0	**0.76**	**0.62**	**0.71**	−0.4	**0.29**	−1.0	−1.0	−1.0
Graminoids‡	−0.11	−0.51	**0.59**	**0.16**	−0.52	−0.82	−1.0	−0.33	−1.0
Carex L., sedge	−1.0	−1.0	−1.0	−1.0	−1.0	−1.0	NA	−1.0	−1.0
Forbs and fern allies									
Maianthemum, mayflower	**0.05**	**0.35**	−0.65	−0.15	−0.87	−0.86	−0.80	−0.80	**0.88**
Aralia, spikenard	NA	NA	−1.0	−0.81	−0.93	−0.79	−1.0	−1.0	**0.96**
Menyanthes, buckbean	NA	−0.47	NA	**0.34**	NA	NA	NA	NA	NA
Clintonia, bluebead	NA	NA	−0.51	**0.00**	−0.83	−0.76	−0.76	−1.0	−1.0
Cornus, dogwood	−0.96	−1.0	−0.98	−0.91	−0.97	−0.99	−1.0	−1.0	−1.0
Equisetum, horsetail	−1.0	−0.20	NA	NA	−0.27	−0.23	**0.79**	−0.16	−1.0
Coptis Salisb., goldthread	NA	NA	−0.80	−1.0	−0.99	−1.0	−1.0	−1.0	−1.0
Anemone L., anemone	−1.0	−1.0	NA	NA	−0.79	−1.0	−1.0	−1.0	−1.0
Aster L., aster	NA	NA	NA	NA	−1.0	−0.83	−1.0	−0.92	−1.0
Hieracium L., hawkweed	NA	NA	NA	NA	NA	NA	−1.0	−0.64	−1.0
Shrubs									
Salix, willow	NA	NA	**0.23**	−1.0	−0.87	−1.0	NA	−1.0	−1.0
Alnus, alder	−1.0	−0.94	−0.91	−0.98	−0.93	−0.99	NA	−1.0	−1.0
Betula, birch	−0.98	−1.0	−1.0	−0.99	NA	NA	NA	−1.0	−1.0
Diervilla, bush honeysuckle	NA	NA	NA	NA	−1.0	**0.48**	NA	NA	NA
Acer L., maple	NA	NA	NA	NA	−0.94	−1.0	−1.0	NA	NA
Lonicera L., honeysuckle	−1.0	−1.0	−0.26	−1.0	−0.39	−1.0	NA	−1.0	−1.0
Rubus L., blackberry	−1.0	−1.0	−1.0	−0.96	−0.99	−0.99	−1.0	−1.0	−1.0
Rosa L., rose	−1.0	−1.0	−1.0	−1.0	−0.85	−0.96	NA	−1.0	−1.0
Linnaea L., twinflower	−1.0	−1.0	−1.0	−1.0	−1.0	−0.99	−0.91	−1.0	−1.0
Ericaceous shrubs									
Ledum, Labrador tea	−1.0	−1.0	−0.87	−0.96	−0.99	−1.0	NA	−1.0	−1.0
Chamaedaphne, leatherleaf	−0.80	−1.0	−0.74	−0.95	NA	NA	NA	NA	−1.0
Vaccinium, blueberry	−1.0	−1.0	−0.88	−1.0	−1.0	−1.0	−0.92	−1.0	−1.0
Mosses									
Sphagnum, sphagnum moss	−0.97	−0.96	−0.98	−0.94	−1.0	−0.99	NA	−1.0	−1.0
Pleurozium, big red stem moss	−1.0	−0.98	−0.93	−0.93	−0.99	−0.99	−0.94	−1.0	−1.0
Ptilium, ptilium moss	−0.55	−1.0	NA	NA	−0.94	−0.98	NA	−1.0	−1.0
Hylocomium, hylocomium feather moss	−1.0	−1.0	−1.0	−1.0	−0.99	−1.0	−1.0	NA	−1.0
Dicranum Hedw., dicranum moss	NA	NA	NA	NA	−1.0	−1.0	−1.0	−1.0	−1.0

Note: NA indicates the species did not occur in the season or cover type. Positive electivities are set in boldface type.
*There were no observations of woodland caribou in mixedwoods in spring.
†There were no observations of caribou in the "disturbed" land classes in summer.
‡Includes grasses and sedges (only some *Carex* spp. were identified).

on our results owing to the narrow diet breath that we recorded among caribou for all study areas and seasons.

Bergerud (1972) reported more than 20 species of plants were commonly eaten during the snow-free seasons in Newfoundland. From his data, we calculated a Levin's diversity index that was more than four times higher than the maximum summer index found for our study, indicating that Newfoundland caribou foraged on a much larger number of items than those in Ontario. Newfoundland caribou foraged year-round on ericaceous shrubs, which comprised 23% of their winter diet, but these species occurred only rarely eaten in Ontario and were not selected in any habitat type. Arboreal lichens were preferred in Newfoundland in winter, with switching to predominantly terrestrial lichens in all other seasons, whereas there was only limited use of arboreal lichens in Ontario. Other differences included a much higher use of sedges, fungi, deciduous shrub leaves, and aquatic macrophytes and lower use of lichens in winter in Newfoundland than we observed in Ontario (Newmaster et al. 2013; this study), or elsewhere in Canada (e.g., Schaefer and Pruitt 1991). Within Ontario, dietary differences occurred among our study areas, primarily during the snow-free periods. These contrasts, across Ontario and between Ontario and Newfoundland, indicated that regional differences exist in diet choice and breadth for woodland caribou, but also that lichens are commonly used in all seasons. Differences in range quality and available food species were also reflected in diet selection by reindeer in Norway (Reimers et al. 1983).

Diet selection was similar in winter and early spring across the province, but differences emerged in late spring and summer, with the selection of a relative few forbs that differed among the study areas. Late-spring and summer diets at all study areas indicated that a mixture of upland and lowland habitats was being used. The most commonly eaten forbs at all study areas were *Maianthemum trifolium* and *Menyanthes trifoliata*, both characteristic of poorly drained soils. Other lowland species, including *Sphagnum* mosses, sedges, and several species of *Equisetum* were also recorded eaten by caribou, suggesting considerable foraging by caribou in bogs and fens in summer, as has been reported elsewhere

in Canada (Rettie and Messier 2000; Lantin et al. 2003; Latham et al. 2011). The continued high use of lichens with few common upland forb species in the summer diet indicated that the upland forest stands were probably selected for their lichen abundance rather than their green-plant abundance, as has also suggested for winter feeding (Johnson et al. 2001; Hins et al 2009). Upland forests, especially open conifer-dominated stands, generally have much higher terrestrial lichen abundance than stands on wetter lowland sites (Kershaw 1977; Crête and Manseau 1996; Grytnes et al. 2006). The fall diet diversity was low, dominated by lichens, and was more similar to winter than to summer. The minimum seasonal diet overlap that we found was still high (65%) because of the predominance of lichens, indicating that terrestrial lichen abundance may strongly influence habitat selection on a year-round basis. Furthermore, selection of foods differed among habitat types, indicating that habitats may be selected for different forage types at landscape and stand scales (Briand et al. 2009; Hins et al. 2009).

We had expected to observe a change in diet from lichens in winter to green plants in spring and summer, and while 50%–60% of the snow-free diet was indeed green plants, this shift was far less exaggerated than we had expected. Bergerud (1972) also reported that <50% of the summer diet was of green plants. Other boreal ungulates, such as moose, correct a negative protein and energy balance acquired over winter by switching entirely from a diet of woody twigs to predominantly green vegetation in summer because of higher protein levels (e.g., Schwartz and Renecker 1998). Few green-plant species were selected: graminoids were selected in spring, possibly because they are among the first plants to grow leaves but were avoided later in summer, and only *Menyanthes* and *Equisetum*, which do not appear until late in June, were selectively eaten from among the many available species, including some highly abundant vernal plants such as *Clintonia* and *Trientalis* L. (starflower). Terrestrial lichens have <4% protein, while some green plants have >30% (Bergerud 1972; Schwartz and Renecker 1998), suggesting that it would be nutritionally beneficial for caribou to reduce their use of lichens in summer. For example, Boertje (1990) reported that a diet that is high in lichens placed caribou in a position of negative nitrogen balance. Graminoids with inflorescences, which were the first green plants available in spring, have high spring protein content (Cebrian et al. 2008). Nevertheless, caribou continued to eat large amounts of terrestrial lichens throughout spring and summer at each of our study areas, highlighting the year-round importance of lichens and suggesting that non-nutritional factors influence caribou foraging choices, given the high availability of higher value green plants in summer. In particular, our electivity patterns suggested suboptimal foraging by female caribou during the parturient period. Storeheier et al. (2002) showed that the capacity of reindeer to digest lichens depended considerably on the species of lichen, with some species preferred over others and the apparent need to consume lichens regularly to maintain the inoculum. Furthermore, lower amounts of lichens in the diet altered or reduced the bacteria needed to digest lichens (Aagnes et al. 1995). These latter results may explain, in part, the year-round consumption of lichens and that certain species are preferred.

Several factors other than forage quality, however, may also influence and constrain habitat and foraging choices by ungulates in boreal forests. Risk of predation has been implicated as a key factor explaining caribou habitat and foraging area decisions, especially for females with calves (Barten et al. 2001; Briand et al. 2009). Insect harassment may cause caribou to seek out habitats with low insect abundance, which could influence diet selection (Downes et al. 1986; Belovsky 1991). The need to maintain a thermal balance may also influence habitat choice and foraging decisions by ungulates in summer and winter (Cook et al. 1998; van Beest et al. 2012), and summer temperature may become critical to boreal caribou under a warming climate regime. Nevertheless, elevated consumption of protein and nutrients in summer is essential to replenish body mass after winter and to increase reproductive success (White 1983; Parker et al. 2009). Regardless of the reason, the continued high intake of lichens throughout the snow-free months could be a key factor constraining caribou calf recruitment (production and calf survival), which is well known to be low for woodland caribou generally (see summary in Brown et al. 2007), and suggests the potential for bottom-up limitation of population growth.

Forest management results in successional habitats within a landscape matrix and so presents different possible diet opportunities for herbivores. Much of the landscape at Nakina remained unharvested and so animals could have restricted habitat selection and foraging to these areas, or they could have taken advantage of the high abundance of forbs in open habitats. Less than 3% of the plants eaten on our managed landscape represented species that are known as abundant in managed successional forests. A higher amount of graminoids was consumed at Nakina in early spring than at Pickle Lake (our unmanaged landscape), and this could be attributed to forest management because grasses are often abundant in recently logged areas (Qi and Scarratt 1998; Martin-DeMoor et al. 2010). The area that had been harvested over the landscape and occupied by caribou at Nakina, however, generally seemed to have had only a minimal influence on diet choice. Therefore, we suspect that the animals behaved similarly to those in managed landscapes elsewhere by largely avoiding disturbed habitats for feeding, probably as a predator avoidance behaviour (Latham et al. 2011; Pinard et al. 2012) or possibly to avoid roads (Pinard et al. 2012; Beauchesne et al. 2013). Lack of data on plant availability from Pickle Lake may have hindered this comparison to some extent; however, the lack of use of abundant species from successional stands suggested that young forests were not used for feeding.

A final factor that we expected might influence diet choice was the presence of a calf because of increased energy demands on the female and vulnerability of the calf to predation (Parker et al. 2009; Pinard et al. 2012). Our sample size of females without calves was too small to test ($N = 4$). In studies where habitat selection for parturition has been reported (Barten et al. 2001; Carr et al. 2011; Pinard et al. 2012), lichens, graminoids, and forbs, which are the main late-spring foods found here, were available suggesting that diet choice might not necessarily be different for caribou with and without calves. Barten et al. (2001) working in montane Alaska found habitat segregation between caribou with and without calves but observed diet similarity, indicating that large-scale habitat choice did not alter food selection. Habitat segregation between females with and without calves has also been recorded in Quebec, but no diet data were reported (Leclerc et al. 2014).

Woodland caribou appear to be obligate lichen foragers and require habitats that supply these foods in abundance, especially because lichen species are grazed selectively and only the tops are consumed. Thus, while there may appear to be an abundance of lichens in boreal forests, such that these foods seem to be not limiting as has been suggested by Courtois et al. (2007), the total available biomass is much smaller than what has been considered previously under the assumption that all lichens could be eaten. Furthermore, as some stands become functionally unavailable owing to disturbances or the presence of predators in disturbed landscapes (Sorensen et al. 2008; Hins et al. 2009), it is possible that lichen availability may well become limiting in a synergistic manner with other factors that restrict habitat use.

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References

Aagnes, T.H., Sørmo, W., and Mathiesen, S.D. 1995. Ruminal microbial digestion in free-living, in captive lichen-fed, and in starved reindeer (*Rangifer tarandus tarandus*) in winter. Appl. Environ. Microbiol. **61**: 583–591. PMID:7574599.

Barten, N.L., Bowyer, R.T., and Jenkins, K.J. 2001. Habitat use by female caribou: tradeoffs associated with parturition. J. Wildl. Manage. **65**: 77–92. doi:10.2307/3803279.

Bastille-Rousseau, G., Schaefer, J.A., Mahoney, S.P., and Murray, D.L. 2013. Population decline in semi-migratory caribou (*Rangifer tarandus*): intrinsic or extrinsic drivers? Can. J. Zool. **91**(11): 820–828. doi:10.1139/cjz-2013-0154.

Beauchesne, D., Jaeger, J.A.G., and St-Laurent, M.-H. 2013. Disentangling woodland caribou movements in response to clearcuts and roads across temporal scales. PLoS ONE, **8**(11): e77514. doi:10.1371/journal.pone.0077514.

Bee, J.N., Wright, D.M., Tanentzap, A.J., Lee, W.G., Lavers, R.B., Mills, J.A., Mark, A.F., and Coomes, D.D. 2010. Spatio-temporal feeding selection of red deer in a mountainous landscape. Austral Ecol. **35**: 752–764. doi:10.1111/j.1442-9993.2009.02082.x.

Belovsky, G.E. 1984. Herbivore optimal foraging: a comparative test of three models. Am. Nat. **124**: 97–115. doi:10.1086/284254.

Belovsky, G.E. 1991. Insights for caribou/reindeer management using optimal foraging theory. Rangifer, **11**(Spec. Issue 7): 7–23. doi:10.7557/2.11.4.987.

Bergerud, A.T. 1972. Food habits of Newfoundland caribou. J. Wildl. Manage. **36**: 913–923. doi:10.2307/3799448.

Berteaux, D., Crete, M., Huot, J., Maltais, J., and Ouellet, J.-P. 1998. Food choice by white-tailed deer in relation to protein and energy content of the diet: a field experiment. Oecologia, **115**: 84–92. doi:10.1007/s004420050494.

Boertje, R.D. 1990. Diet quality and intake requirements of adult female caribou of the Denali herd, Alaska. J. Appl. Ecol. **27**: 420–424. doi:10.2307/2404291.

Briand, Y., Ouellet, J.-P., Dussault, C., and St-Laurent, M.-H. 2009. Fine-scale habitat selection by female forest-dwelling caribou in managed boreal forest: empirical evidence of a seasonal shift between foraging opportunities and anti-predator strategies. Ecoscience, **16**: 330–340. doi:10.2980/16-3-3248.

Brown, G.S., Landriault, L., Sleep, D.J.H., and Mallory, F.F. 2007. Comment arising from a paper by Wittmer et al.: hypothesis testing for top-down and bottom-up effects in woodland caribou population dynamics. Oecologia, **154**: 485–492. doi:10.1007/s00442-007-0855-3.

Canadian Council on Animal Care. 2003. Guidelines on the care and use of wildlife. Canadian Council on Animal Care, Ottawa, Ont.

Carleton, T.J. 2000. Vegetation responses to the managed forest landscape of central and northern Ontario. *In* Ecology of a managed terrestrial landscape: patterns and processes of forest landscapes in Ontario. *Edited by* A.H. Perera, D.L. Euler, and I.D. Thompson. UBC Press, Vancouver, B.C. pp. 178–197.

Carr, N.L., Rodgers, A.R., Kingston, S.R., and Lowman, D.J. 2011. Use of island and mainland shorelines by woodland caribou during the nursery period in two northern Ontario parks. Rangifer, **31**(Spec. Issue 19): 41–54. doi:10.7557/2.31.2.1989.

Cebrian, M.R., Kielland, K., and Finstad, G. 2008. Forage quality and reindeer productivity: multiplier effects amplified by climate change. Arc. Antarct. Alp. Res. **40**: 48–54. doi:10.1657/1523-0430(06-073)[CEBRIAN]2.0.CO;2.

Chen, H.Y.H., and Popadiouck, R.V. 2002. Dynamics of North American boreal mixedwoods. Environ. Rev. **10**(3): 137–166. doi:10.1139/a02-007.

Cook, J.G., Irwin, L.L., Bryant, L.D., Riggs, R.A., and Thomas, J.W. 1998. Relations of forest cover and condition of elk: a test of the thermal cover hypothesis in summer and winter. Wildl. Monogr. **141**: 1–61.

Courtois, R., Ouellet, J.-P., Breton, L., Gingras, A., and Dussault, C. 2007. Effects of forest disturbance on density, space use, and mortality of woodland caribou. Ecoscience, **14**: 491–498. doi:10.2980/1195-6860(2007)14[491:EOFDOD]2.0.CO;2.

Crête, M., and Manseau, M. 1996. Natural regulation of Cervidae along a 1000 km latitudinal gradient: change in trophic dominance. Evol. Ecol. **10**: 51–62. doi:10.1007/BF01239346.

Cringan, A.T. 1957. History, food habits and range requirements of the woodland caribou of continental North America. Trans. N. Am. Wildl. Conf. **22**: 485–500.

Dailey, T.V., Hobbs, N.T., and Woodward, T.N. 1984. Experimental comparisons of diet selection by mountain goats and mountain sheep in Colorado. J. Wildl. Manage. **48**: 799–806. doi:10.2307/3801426.

Danell, K., and Ericson, L. 1986. Foraging by moose on two species of birch when these occur in different proportions. Holarct. Ecol. **9**: 79–84.

Downes, C.M., Theberge, J.B., and Smith, S.M. 1986. The influence of insects on the distribution, microhabitat choice, and behaviour of the Burwash caribou herd. Can. J. Zool. **64**(3): 622–629. doi:10.1139/z86-092.

Ferguson, S.H., and Elkie, P.C. 2004. Habitat requirements of boreal forest caribou during the travel seasons. Basic Appl. Ecol. **5**: 465–474. doi:10.1016/j.baae.2004.04.011.

Festa-Bianchet, M., Ray, J.C., Boutin, S., Côté, S.D., and Gunn, A. 2011. Conservation of caribou (*Rangifer tarandus*) in Canada: an uncertain future. Can. J. Zool. **89**(5): 419–434. doi:10.1139/z11-025.

Forsyth, D.M., Richardson, S.J., and Menchenton, K. 2005. Foliar fibre predicts diet selection by invasive red deer *Cervus elaphus scoticus* in a temperate New Zealand forest. Funct. Ecol. **19**: 495–504. doi:10.1111/j.1365-2435.2005.00991.x.

Grytnes, J.-A., Heeguaard, H., and Ihlen, P.G. 2006. Species richness of vascular plants, bryophytes and lichens along an altitudinal gradient in western Norway. Acta Oecol. **29**: 241–246. doi:10.1016/j.actao.2005.10.007.

Gustine, D.D., Barboza, P.S., Lawler, J.P., Adams, L.G., Parker, K.L., Arthur, S.M., and Schults, B.S. 2012. Diversity of nitrogen isotopes and protein status in caribou: implications for monitoring northern ungulates. J. Mammal. **93**: 778–790. doi:10.1644/11-MAMM-A-164.1.

Hins, C., Ouellet, J.-P., Dussault, C., and St-Laurent, M.-H. 2009. Habitat selection by forest-dwelling caribou in managed boreal forest of eastern Canada: evidence of a landscape configuration effect. For. Ecol. Manage. **257**: 636–643. doi:10.1016/j.foreco.2008.09.049.

Johnson, C.J., Parker, K.L., and Heard, D.C. 2001. Foraging across a variable landscape: behavioral decisions made by woodland caribou at multiple spatial scales. Oecologia, **127**: 590–602. doi:10.1007/s004420000573.

Kershaw, K.A. 1977. Studies on lichen-dominated systems. XX. An examination of some aspects of the northern boreal lichen woodlands in Canada. Can. J. Bot. **55**(4): 393–410. doi:10.1139/b77-050.

Lantin, É., Drapeau, P., Paré, M., and Bergeron, Y. 2003. Preliminary assessment of habitat characteristics of woodland caribou calving areas in the Claybelt region of Québec and Ontario, Canada. Rangifer, **23**(Spec. Issue 14): 247–254. doi:10.7557/2.23.5.1708.

Latham, A.D.M., Latham, M.C., and Boyce, M.S. 2011. Habitat selection and spatial relationships of black bears (*Ursus americanus*) with woodland caribou (*Rangifer tarandus caribou*) northeastern Alberta. Can. J. Zool. **89**(4): 267–277. doi:10.1139/z10-115.

Leclerc, M., Dussault, C., and St-Laurent, M.-H. 2014. Behavioural strategies towards human disturbances explain individual performance in woodland caribou. Oecologia, **176**: 297–306. doi:10.1007/s00442-014-3012-9. PMID:25034087.

Lenart, E.A., Bowyer, R.T., Ver Hoef, J., and Ruess, R.W. 2002. Climate change and caribou: effects of summer weather on forage. Can. J. Zool. **80**(4): 664–678. doi:10.1139/z02-034.

Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, N.J.

Martin-DeMoor, J., Lieffers, V.J., and Macdonald, S.E. 2010. Natural regeneration of white spruce in aspen-dominated boreal mixedwoods following harvesting. Can. J. For. Res. **40**(3): 585–594. doi:10.1139/X10-016.

McMullin, R.T., Thompson, I.D., Lacey, B.W., and Newmaster, S.G. 2011. Estimating the biomass of woodland caribou forage lichens. Can. J. For. Res. **41**(10): 1961–1969. doi:10.1139/x11-108.

Mysterud, A. 2000. The relationship between ecological segregation and sexual body size dimorphism in large herbivores. Oecologia, **124**: 40–54. doi:10.1007/s004420050023.

Newman, J.A., Parsons, A.J., Thornley, J.H.M., Penning, P.D., and Krebs, J.R. 1995. Optimal diet selection by a generalist grazing herbivore. Funct. Ecol. **9**: 255–268. doi:10.2307/2390572.

Newmaster, S.G., Thompson, I.D., Steeves, R.A.D., Rodgers, A.R., Fazekas, A.J., Maloles, J.R., McMullin, R.T., and Fryxell, J.M. 2013. Examination of two new technologies to assess the diet of woodland caribou: video recorders attached to collars and DNA barcoding. Can. J. For. Res. **43**(10): 897–900. doi:10.1139/cjfr-2013-0108.

Ontario Ministry of Natural Resources. 2000. Provincial Land Cover database (PLC 2000). 2nd ed. Ontario Ministry of Natural Resources, Toronto.

Owen-Smith, N., and Novellie, P. 1982. What should a clever ungulate eat? Am. Nat. **119**: 151–178. doi:10.1086/283902.

Parker, K.L., Barboza, P.S., and Gillingham, M.P. 2009. Nutrition integrates environmental responses of ungulates. Funct. Ecol. **23**: 57–69. doi:10.1111/j.1365-2435.2009.01528.x.

Parker, K.L., Barboza, P.S., and Stephenson, T.R. 2005. Protein conservation in female caribou (*Rangifer tarandus*): effects of decreasing diet quality during winter. J. Mammal. **86**: 610–622. doi:10.1644/1545-1542(2005)86[610:PCIFCR]2.0.CO;2.

Pinard, V., Dussault, C., Ouellet, J.-P., Fortin, D., and Courtois, R. 2012. Calving rate, calf survival rate, and habitat selection of forest-dwelling caribou in a highly managed landscape. J. Wildl. Manage. **76**: 189–199. doi:10.1002/jwmg.217.

Post, E., and Klein, D.R. 1999. Caribou calf production and seasonal range quality during a population decline. J. Wildl. Manage. **63**: 335–345. doi:10.2307/3802517.

Post, E., Pedersen, C., Wilmers, C.C., and Forchhammer, M.C. 2008. Warming, plant phenology and the spatial dimension of trophic mismatch for large herbivores. Proc. R. Soc. Lond. B Biol. Sci. **275**: 2005–2013. doi:10.1098/rspb.2008.0463.

Qi, M., and Scarratt, J.B. 1998. Effect of harvesting method on seed bank dynam-

ics in a boreal mixedwood forest in northwestern Ontario. Can. J. Bot. **76**(5): 872–883. doi:10.1139/b98-061.

Reimers, E., Klein, D.R., and Sørungaard, R. 1983. Calving time, growth rate, and body size of Norwegian reindeer on different ranges. Arct. Alp. Res. **15**: 107–118. doi:10.2307/1550986.

Renecker, L.A., and Schwartz, C.C. 2007. Food habits and feeding behavior. *In* Ecology and management of the North American moose. *Edited by* A.W. Franzmann, C.C. Schwartz, and W. McCabe. University of Colorado Press, Denver. pp. 403–439.

Rettie, W.J., and Messier, F. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. Ecography, **23**: 466–478. doi:10.1111/j.1600-0587.2000.tb00303.x.

Rominger, E.M., Robbins, C.T., and Evans, M.A. 1996. Winter foraging ecology of woodland caribou in northeastern Washington. J. Wildl. Manage. **60**: 719–728. doi:10.2307/3802370.

Rowe, J.S. 1972. The forest regions of Canada. Publ. No. 1300. Canadian Forestry Service, Ottawa, Ont.

Schaefer, J.A., and Pruitt, W.O. 1991. Fire and woodland caribou in southeastern Manitoba. Wildl. Monogr. **116**: 1–39.

Schoener, T.W. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology, **51**: 408–418. doi:10.2307/1935376.

Schwartz, C.C., and Renecker, L.A. 1998. Nutrition and energetics. *In* Ecology and management of the North American moose. *Edited by* A.W. Franzmann and C.C. Schwartz. Smithsonian Institution Press, Washington, D.C. pp. 441–478.

Seip, D.R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. Can. J. Zool. **70**(8): 1494–1503. doi:10.1139/z92-206.

Skogland, T. 1991. What are the effects of predators on large ungulate populations? Oikos, **61**: 401–411. doi:10.2307/3545248.

Sleep. D.J.H. 2007. State of knowledge and analysis of current research on woodland caribou in Canada. Nat. Coun. Air Stream Improve. (NCASI) Tech. Bull. No. 939.

Sorensen, T., McLoughlin, P.D., Hervieux, D., Dzus, E., Nolan, J., Wynes, B., and Boutin, S. 2008. Determining sustainable levels of cumulative effects for boreal caribou. J. Wildl. Manage. **72**: 900–905. doi:10.2193/2007-079.

Staines, B.W., Crisp, J.M., and Parish, T. 1982. Differences in the quality of food eaten by red deer (*Cervus elaphus*) stags and hinds in winter. J. Appl. Ecol. **19**: 65–77. doi:10.2307/2402991.

Storeheier, P.V., Mathiesen, S.D., Tyler, N.J.C., and Olsen, M.A. 2002. Nutritive value of terricolous lichens for reindeer in winter. Lichenologist, **34**: 247–257. doi:10.1006/lich.2002.0394.

Thomas, D.C., Edmonds, E.J., and Brown, W.K. 1994. The diet of woodland caribou populations in west-central Alberta. Rangifer, **16**(Spec. Issue 9): 337–342. doi:10.7557/2.16.4.1275.

Thompson, D.P., and Barboza, P.S. 2013. Responses of caribou and reindeer (*Rangifer tarandus*) to acute food shortages in spring. Can. J. Zool. **91**(9): 610–618. doi:10.1139/cjz-2013-0047.

Thompson, I.D., Bakhtiari, M., Rodgers, A.R., Baker, J.A., Fryxell, J.M., and Iwachewski, E. 2012. Application of a high-resolution animal-borne remote video camera with global positioning for wildlife study: observations on the secret lives of woodland caribou. Wildl. Soc. Bull. **36**: 365–370.

Trudell, J., and White, R.G. 1981. The effect of forage structure and availability on food intake, biting rate, bite size and daily eating time of reindeer. J. Appl. Ecol. **18**: 63–81. doi:10.2307/2402479.

van Beest, F.M., Van Moorter, B., and Milner, J.M. 2012. Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate. Anim. Behav. **84**: 723–735. doi:10.1016/j.anbehav.2012.06.032.

Vanderploeg, H.A., and Scavia, D. 1979. Calculation and use of selectivity coefficients of feeding: zooplankton grazing. Ecol. Model. **7**: 135–149. doi:10.1016/0304-3800(79)90004-8.

Walsh, N.E., McCabe, T.R., Welker, J.M., and Parsons, A.N. 1997. Experimental manipulations of snow depth: effects on nutrient content of caribou forage. Glob. Change Biol. **3**(Suppl. 1): 158–164. doi:10.1111/j.1365-2486.1997.gcb142.x..

White, R.G. 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. Oikos, **40**: 377–384. doi:10.2307/3544310.

Williams, B.K., and Titus, K. 1988. Assessment of sampling stability in ecological applications of discriminant analysis. Ecology, **69**: 1275–1285. doi:10.2307/1941283.

Wittmer, H.U., Sinclair, A.R.E., and McLellan, B.N. 2005. The role of predation in the decline and extirpation of woodland caribou. Oecologia, **144**: 257–267. doi:10.1007/s00442-005-0055-y.

Zweifel-Schielly, B., Leusenberger, Y., Kreuzer, M., and Suter, W. 2012. A herbivore's food landscape: seasonal dynamics and nutritional implications of diet selection by a red deer population in contrasting alpine habitats. J. Zool. (Lond.), **286**: 68–80. doi:10.1111/j.1469-7998.2011.00853.x.